BENTHIC PRODUCTIVITY OF A WETLAND POND

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BENTHIC PRODUCTIVITY OF A WETLAND POND

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SUMMARY

This is an investigation of the secondary production of two benthic crustacean populations, Asellus obtusus (Isopoda, Asellidae) and Crangonyx gracilis (Amphipoda, Gammaridae), found in a small wetland pond in northwest Georgia. Two distinct habitat zones were delineated within the study site, a central Cephalanthus occidentalis zone and a marginal Nyssa biflora zone. Benthic samples taken in random sections of the pond indicated that the great majority of crustaceans existed in the shallow Nyssa benthic habitat and in the aufwuchs habitat of both zones. Replicated monthly samples were taken from the Nyssa benthic habitat and the aufwuchs habitat in both the Nyssa and Cephalanthus zones over a one year period. Comparisons of crustacean production were made on a unit area of bottom basis between the Nyssa and Cephalanthus zones. The Hynes and Coleman method of assessing secondary production as modified by Hamilton was used in estimating amphipod and isopod annual production in terms of dry weight. The Crangonyx annual production in the Nyssa zone (benthos and aufwuchs) was estimated to be 2.44 g/m^2 from a mean annual standing crop of .4 g/m^2 (turnover ratio = 6.1) and in the Cephalanthus zone (aufwuchs only), 1.64 g/m^2 from a mean annual standing crop of .23 g/m^2 (turnover ratio = 7.1). Asellus annual production was 1.43 g/m^2 in the Nyssa zone (benthos and

aufwuchs) from a mean annual standing crop of .24 g/m^2 (turnover ratio = 5.9) and .65 g/m^2 from a mean annual standing crop of .08 g/m^2 (turnover ratio = 8.1) in the Cephalanthus zone (aufwuchs only). There is a strong possibility that the production values are underestimates but they are comparable to production estimates of related species. Production comparisons showed the aufwuchs to be a significant contributor to the total community metabolism.

CHAPTER I

INTRODUCTION

Wetlands are among the world's richest ecosystems, in terms of both productivity and diversity of species (Helfgott, et al, 1973). Many problems of wetland management derive from the fact that little is known about ecological processes in most of these systems. This is primarily due to the difficulty of studying such large complex ecosystems. The majority of wetland studies has been concerned with coastal wetlands, chiefly tidal marshes (Pomeroy 1959, Odum 1961, Teal 1962, Reimold 1972, and Brickman 1972). Although there is an increasing amount of attention being focused on inland wetlands, most of the work to date has been descriptive in nature (Klein, et al, 1970, Whitehead 1972, and Carter, et al, 1973) and little is known about the functional aspects of these systems.

Wetland systems exhibit a detritus-based energy flow (Odum, 1971). The majority of the energy is derived from the active decomposition of organic matter by the detritivores and saprophages such as bacteria, molds, yeasts, fungi, and many forms of benthic invertebrates. Predation upon these forms is the mechanism by which the majority of energy is passed through the food webs. The elaboration of organic matter by all consumers is termed secondary production. Since the benthic invertebrates form a critical link in the detritus food chain, the study of benthic secondary production is especially important in understanding energy flow and nutrient cycling. Furthermore, it is important in fishery management and may be important in assessing the capacity of natural wetland systems to assimilate large amounts of organic wastes as Wharton (1970) has indicated.

The present study is an investigation of the production process of the two dominant invertebrate populations, Asellus obtusus (Isopoda, Asellidae), and Crangonyx gracilis (Amphipoda, Gammaridae) occurring in one of many small shallow wetland ponds in Bartow County, Georgia, approximately 60 miles northwest of Atlanta. These ponds are unique ecosystems and were designated by the Georgia Natural Areas Council as worthy of acquisition by the State for preservation. Greear (1967) studied the zonation of vegetation in and around several of the ponds and termed them "Sag Ponds" because they apparently originated when the underlying limestone dissoluted causing the ground to "sag". The material overlying the limestone is impervious and water collects in the depressions forming the ponds. Three concentric zones of vegetation were delineated within the study site, Bob Black Pond; a central Cephalanthus occidentalis (buttonbush) zone, an intermediate open water zone (no emergent vegetation), and an outer Nyssa biflora (black gum) zone (Figure 1). Beyond the pond margin and sometimes extending into the pond is an Acer rubrum-Lynia lucida (red maple-fetterbush) zone. Radiocarbon dating of the pollen assemblages from the sediments indicate the age of Bob Black Pond to be 22,900$\pm$400 years before present (Watts, 1969). This would place the orgin of the pond in the last full-glacial period.

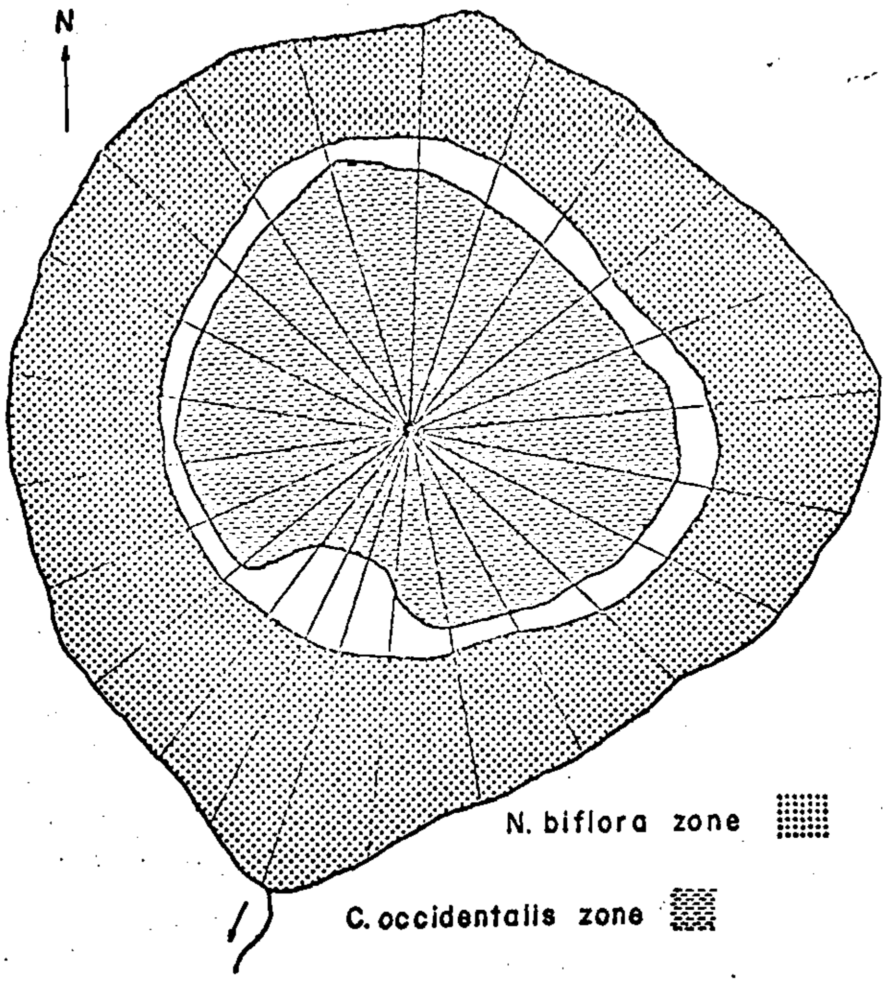

Figure 1. Map of Bob Black Pond Showing the Nyssa biflora Zone, the Cephalanthus occidentalis Zone and the Sampling Sections.

CHAPTER II

PROCEDURE

The sampling system was designed in the following manner. The pond was divided into 23 triangular sections with the apex of each section at the center of the pond and the pond margin forming the base (Figure 1). As the vegetational zones are concentric, each section encompasses a portion of each of the zones. Five sections were randomly selected for sampling each time a trip was made. Initially, three benthic samples were taken from each of the five sections, one from the *Cephalanthus* zone, one from the open water zone, and one from the *Nyssa* zone. This then provided five replicate samples from each of the vegetational zones, giving a total of 15 samples per date.

This design was modified after the first set of samples was taken (July, 1973) when it was apparent that very few animals were present in the open water and *Cephalanthus* zones and a large number of animals were observed clinging to submerged mosses on the trees and buttonbush. The modification was made in order to determine spatial distribution and density of the periphytic or "aufwuchs" (Ruttner, 1963) populations. One benthic sample continued to be taken in the *Nyssa* zone in each of five sections, but benthic sampling of the *Cephalanthus* zone and open water zone was discontinued. In addition to the benthic sample, two aufwuchs samples were taken in each section, one from the *Nyssa* zone and one from the *Cephalanthus* zone, giving a total of 10 aufwuchs samples per date.

Samples were collected near the end of each month at monthly intervals (except January 15) from July, 1973 through June, 1974. Benthic samples were collected with an Ekman grab (225 cm^2) mounted on a pole. The aufwuchs samples were taken with a sampling device designed by the author. This device is constructed of nylon meshing (43 meshes per cm, 153 micron aperture) fashioned into an open-end cylinder 20 centimeters in length capable of encompassing tree trunks or shrubs 5-10 centimeters in diameter. The cylinder may be opened and closed by means of a strip of Velcro tape running the length of the cylinder. The ends may be secured through the use of drawstrings at either end. In order to take an aufwuchs sample one must open the cylinder, place it around the tree trunk above the water level and close it. The uppermost end of the cylinder is then drawn tight around the trunk and secured. Holding the bottom end of the sampler open, the device is pulled down the trunk into the water until the upper end is flush with the water level. The botton end is then closed around the tree trunk and the area within the device is agitated to dislodge any animals clinging to the tree trunk. The sampler is then removed from the water by sliding it up the trunk, taking care that the ends remain tightly secured, and the sample is removed. Caution must be exercised in removing the device so that as much of the periphytic plant growth as possible is removed from the area sampled.

The samples were transported back to the laboratory at Georgia Tech in plastic buckets. Using a #50 sieve (.28 mm aperture) and the sugar flotation technique of Anderson (1959), the samples were washed and sorted, and then stored in 70% ethyl alcohol for later counting.

Head length frequency was used to analyze the age structure of the _Crangonyx_ population as Cooper (1965) found that the head length of of the amphipod _Hyallela azteca_ was a suitable aging criterion. Ten size classes of .08 mm intervals were arbitrarily selected in constructing the size frequency histograms. The only criterion used in past work on _Asellus_ has been total body length (Ellis 1961, Andersson 1969). It was felt that since total body length could be affected by compression or other mechanisms, particularly in animals preserved for two to three months, a more rigid structure should be used as an age determinant. As the abdomen of the isopod is a rigid chelicerated structure, it was decided to use abdominal width frequency to determine the age structure of the isopod population. Fifteen size classes of .20 mm were arbitrarily selected to construct the size frequency histograms. All of the size frequency measurements were made with a Bausch and Lomb Stereo-Zoom 7 dissecting microscope equipped with an ocular micrometer disc accurate to .02 mm at 50X magnification.

Dry weight biomass was determined for the _Asellus_ and _Crangonyx_ populations. Animals from samples taken specifically for this purpose were sorted into appropriate size groups and these groups were oven dried at 85°C for approximately 16 hours. A Mettler 5-place (H64) balance was used in the weight determinations. Animals were weighed according to size group and the reading, divided by the number of animals in that particular size group, provided the mean individual dry weight in milligrams. Regression analyses then provided a conversion factor for each size category of each species.

In order to convert all densities to the same units, number per square meter of bottom area, the aufwuchs area per square meter of bottom area had to be determined. For the *Cephalanthus* zone, 10 random one square meter quadrats provided an estimate of the mean number of shrubs per square meter of bottom. By obtaining the mean number of animals per shrub or stem, one could then estimate the mean number of animals per square meter of bottom.

To determine area of aufwuchs habitat per square meter of bottom in the shallow *Nyssa* zone, eight representative quadrats were selected ranging in size from 52 m^2 to 15 m^2. The variation was due to the relative width of the *Nyssa* zone in different portions of the pond. The trees in each of these quadrats were counted and their circumference recorded. As the aufwuchs sampler only sampled a 20 cm length of tree and the animals were confined to this zone, this distance in length in combination with the circumference was used to compute total tree area in each quadrat. The total tree area divided by the total quadrat area then gave an estimate of the tree area per square meter of bottom. The mean from these eight estimates provided a conversion factor to convert tree densities to bottom densities.

Hamilton's (1969) modification of the Hynes and Coleman (1968) method for assessing secondary production of benthos was used in estimating crustacean production. This method allows the estimation of production of populations in which specific cohorts cannot be identified. The total age distribution of the population collected over the year is categorized according to size classes. This annual distribution is then divided by the number of sampling dates to approximate an "average ideal cohort" (Hamilton, 1969). Losses between adjacent size classes may be attributed to mortality, and the corrected sum of losses is equivalent to annual production. It is not the loss from each size class that is so important but the sum of losses of all size classes.

Oxygen measurements were taken at each sampling site when possible using a YSI Model 54 Oxygen Meter. Oxygen readings were also taken in deep water to monitor profundal oxygen fluctuations. All oxygen measurements were taken at approximately 11 a.m. regardless of the sampling date. Diurnal oxygen fluctuations were measured July 20-21, 1974, at two hour intervals. This data was plotted in order to assess the effect of respiratory and photosynthetic activities on oxygen concentrations. Other physico-chemical data were collected using a Hach field kit for limnological measurements.

CHAPTER III

RESULTS

Characteristics of Aquatic Habitat

Bob Black Pond is a shallow "blackwater" system that is in an advanced state of natural eutrophication, perhaps tending toward dystrophy. The pond is about 0.5 hectare in size lying at the bottom of a topographical depression. There is one outlet that flows in periods of high water to an adjacent pond some 30 meters away. It appears that all of the water entering Bob Black Pond must come from its small circular watershed which is about 150 meters in diameter (Greear, 1967). The deeper portions of the pond are about 1-1.5 meters and the average depth is less than a meter. Field tests indicated the pond to be acidic (pH 5.4-6.0) and low in total hardness (20 mg/l as calcium carbonate). Temperature ranged from 7°-$28^{\circ}C$. Oxygen concentrations near the surface ranged from less than 1 mg/l in the late summer to about 10 mg/l in the early spring. Deeper portions of the pond became almost anoxic during late summer and fall. Oxygen readings taken at each sampling site indicated that for the greater part of the year the aufwuchs and Nyssa benthic concentrations were higher (1.0-9.4 mg/l) than the benthic concentrations in the Cephalanthus and open water zones (0.5-1.4 mg/l).

A diurnal oxygen curve (Figure 2) indicated that oxygen concentrations in the aufwuchs and benthic habitat reached a maximum of 4.5-6.0 mg/l in the late afternoon and declined to less than 1.0 mg/l by 6 a.m. The profundal oxygen concentrations remained very low regardless of time of day.

Water level measurements indicated a 50 cm difference between minimum pool in September-October and maximum pool in January. Minimum, maximum, and average pool area measurements were made. These indicated that the *Nyssa* zone had an area of 3685 m^2 at maximum level, 3015 m^2 at average level, and 2211 m^2 at minimum water level. The *Cephalanthus* zone had an area of 530 m^2 regardless of the height of the water level.

The invertebrate biota of the pond is very diverse with groups such as the Coleoptera, Hemiptera, Odonata (Libellulidae), Diptera (Culicidae, Chironomidae), Hydracarina, and Annelida well represented. The greatest part of the benthic invertebrate biomass is composed of two crustacean populations, an isopod, *Asellus obtusus*, and an amphipod, *Crangonyx gracilis*. The majority of the remaining biomass is made up of the chironomids and the odonates. The top predaceous fish in this system are mosquitefish (*Gambusia* sp.), sunfish (*Lepomis* sp.), and pickerel (*Esex* sp.).

The pond is subject to algal blooms in the spring. Large masses of filamentous algae float on the surface buoyed by gas bubbles. These

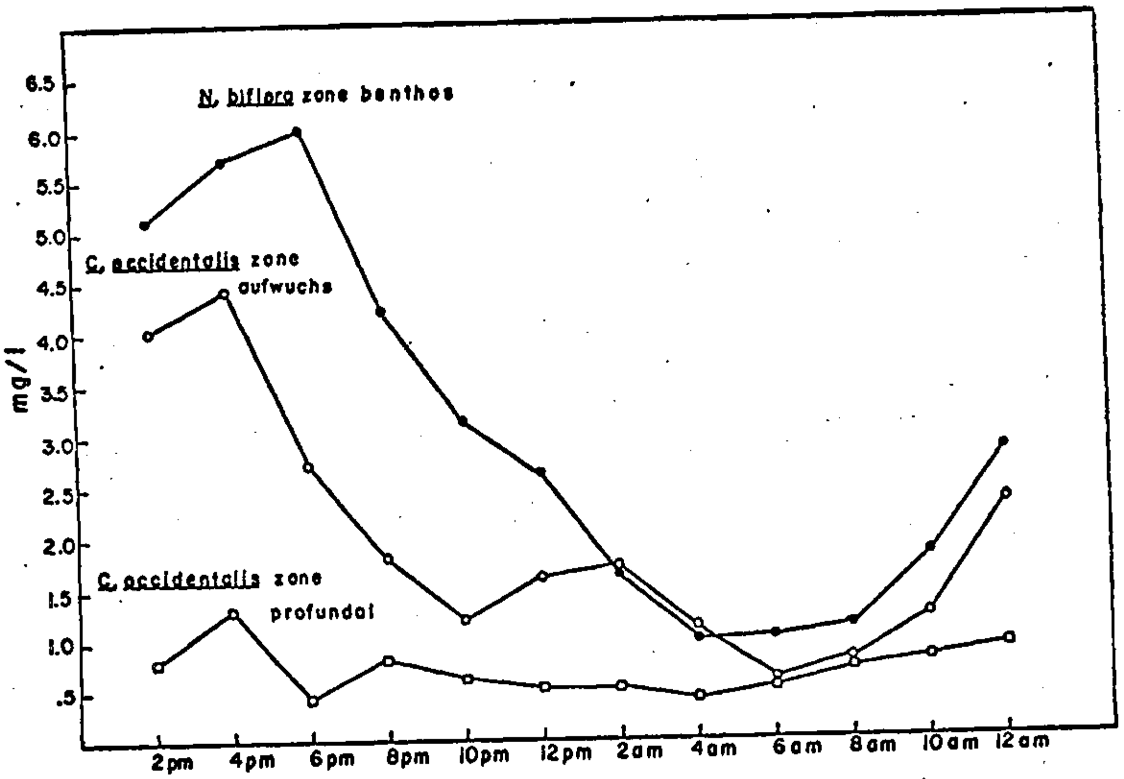

Figure 2. Comparison of Diurnal Oxygen Curves Taken July 20-21, 1974 at Two Hour Intervals in the Benthos of the Nyssa biflora Zone, the Aufwuchs of the Cephalanthus occidentalis Zone and the Profundal Zone of the Cephalanthus occidentalis Zone.

mats are predominately Spirogyra with other filamentous algae intermixed. Gelatinous algal masses also grow on submerged objects and may form spherical masses 8-10 centimeters in diameter. Most of the submerged objects (tree trunks, shrubs, logs) support a healthy growth of mosses and algae. This epiphytic growth extends from the water level to about 20 cm down on vertical objects such as trees and shrubs. There are some areas where acid-water macrophytes, Potamogeton sp. and Sphagnum sp., flourish.

Age Structure and Life Histories of Species

Size frequency distributions of each zone for each sampling date indicated only minor variations between habitats. Therefore, the distributions were combined to give an estimate of the age structure of the total population for each sampling date and these used in elucidating life cycles (Figures 3 and 4).

The amphipod, Crangonyx gracilis, has a life cycle that appears to span about one year. Generally, the new generation appears in February (Figure 3) with about 48% of the animals sampled being in the first size class. Measurements of newly hatched individuals indicated the head length of first instar animals to be in the range of .26-.32 mm. The age structure does not change appreciably through the spring except for the steady disappearence of the older adults. Reproduction continues, although at a lower level, through October after which no animals appear

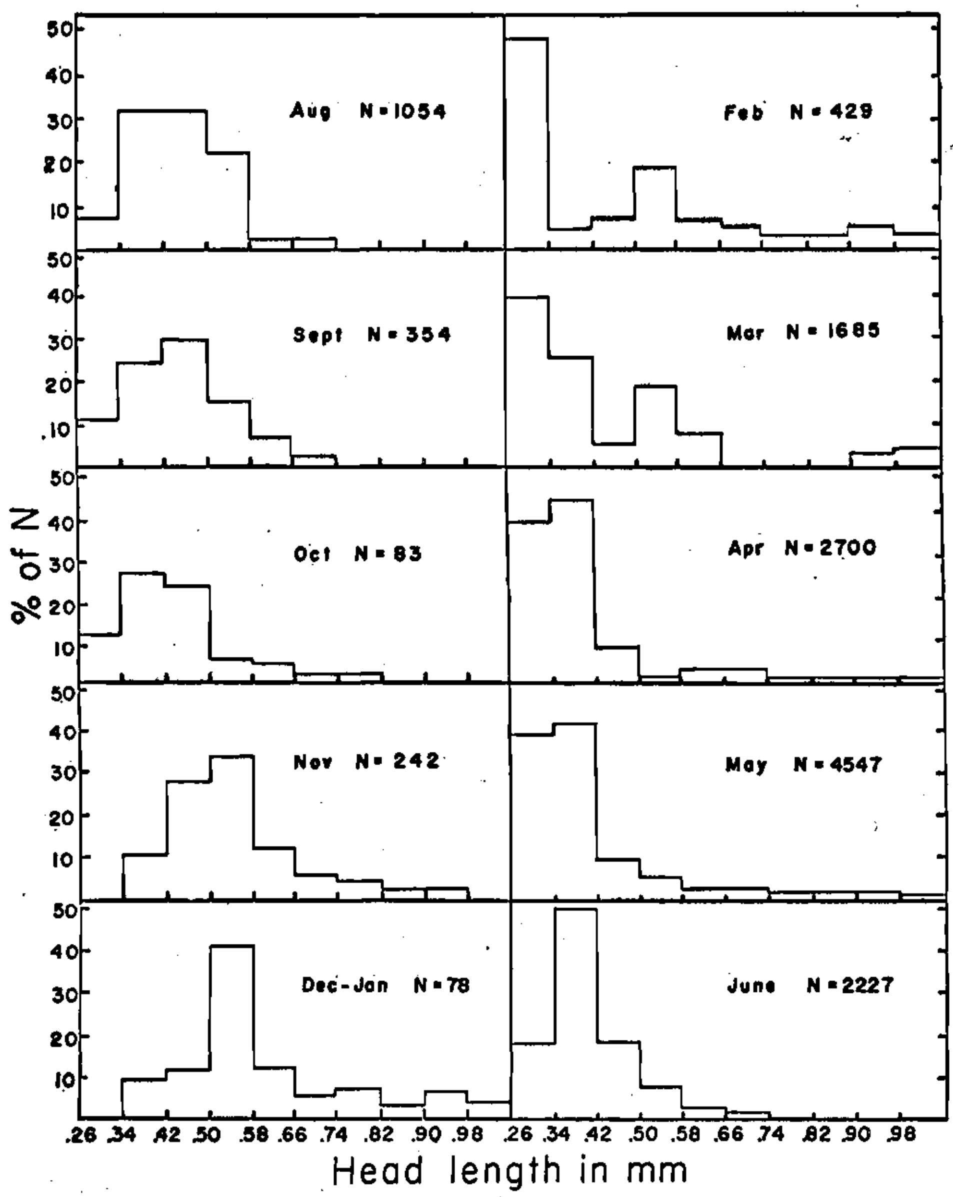

Figure 3. Monthly Size Frequency Distribution of Crangonyx gracilis Showing Percentage of Total Number of Animals in each Size Class Collected each Sampling Date.

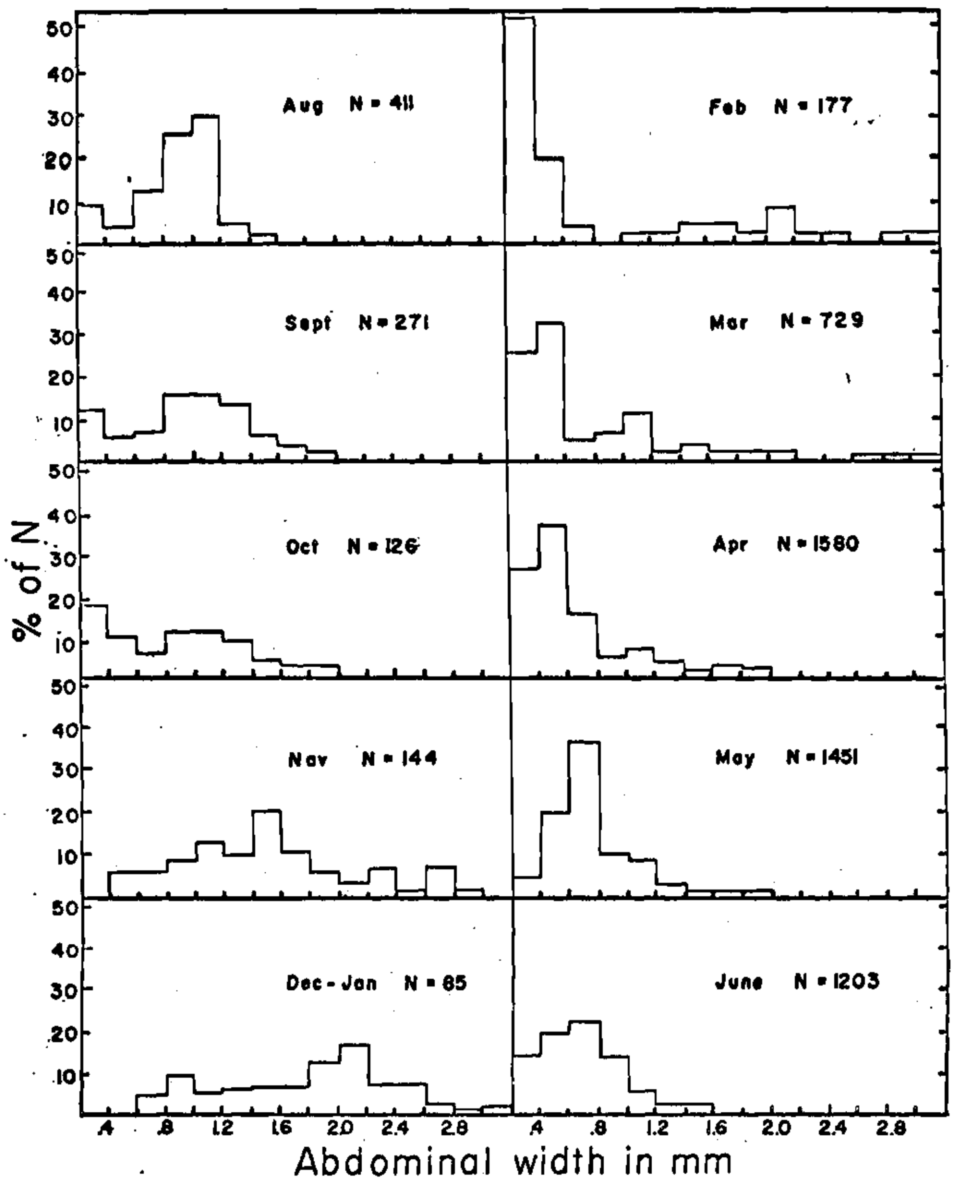

Figure 4. Monthly Size Frequency Distribution of Asellus obtusus Showing Percentage of Total Number of Animals in each Size Class Collected each Sampling Date.

in the first size class. This long reproductive period may be due in some part to the breeding of spring individuals who have matured over the summer. Since reproductive maturity is attained when the animals reach the fifth size class (.58-.66 mm head length) this is probably true to some extent. The animals surviving at the onset of winter remain in the population to give rise to the next spring generation after which they presumably die.

Asellus obtusus has a similar life history that appears to span one year. Hatching of the spring generation begins in February (Figure 4) with about 53% of the animals collected being in the first size class. First instar animals have an abdominal width in the range of .26-.32 mm as indicated by measurement of newly hatched individuals. Hatching continues at a high rate through April. By May the rate of reproduction has decreased but it remains continuous through October. The long reproductive period is probably due in part to late summer reproduction by mature individuals of the spring generation. Since reproductive maturity is attained when the isopods reach the fifth size class (1.0-1.20 mm abdominal width), this is probably true. By November no animals are found in the first size class and animals surviving at the onset of winter remain in the population to give rise to the next spring generation after which they disappear from the population.

Spatial Distribution

The initial set of benthic samples taken July 27, 1973, indicated that practically no isopods or amphipods existed in the benthos of the *Cephalanthus* zone or the open water zone. Most of the benthic invertebrates found in these zones were either chironomid larvae or *Chaoborus*. The July benthic samples indicated a mean amphipod density of $203/m^2$ in the open water zone and zero in the *Cephalanthus* zone. At the same time the mean benthic density in the *Nyssa* zone was $5181/m^2$. Isopod benthic densities were $26/m^2$ in the open water zone and zero in the *Cephalanthus* zone. The mean benthic density in the *Nyssa* zone for this date was $1500/m^2$. An analysis of variance indicated a significant difference in crustacean densities among vegetational zones at a probability level of .01. Two benthic samples taken in February, April, May, and June of 1974 from each of the deep zones indicated a continuous low density throughout the sampling period.

The manner in which the ecosystem is structured suggested combining the aufwuchs and benthic habitat in the *Nyssa* zone, for purposes of population and productivity analyses, and comparing this with the aufwuchs habitat in the *Cephalanthus* zone. The *Nyssa* zone was found to have .1 m^2 of aufwuchs habitat per square meter of bottom and this was used to convert aufwuchs densities to the same units as benthic samples. The aufwuchs densities in the *Nyssa* zone were quite substantial compared to the *Nyssa* benthic densities on a unit area of habitat basis

(Figures 5 and 6). In the spring the aufwuchs densities were considerably higher than the benthic densities on this basis. However, after converting aufwuchs densities to a unit area of bottom basis for comparative purposes, the aufwuchs densities were drastically reduced.

A density of 17 Cephalanthus stems per square meter of bottom was used in converting aufwuchs densities to number per square meter of bottom in this zone. It was assumed that all of the Cephalanthus had an equal surface area since most of the shrubs, large and small, had roughly the same amount of epiphytic growth on the submerged portions. The aufwuchs densities in the Cephalanthus zone (Figures 7 and 8) were much greater than the Nyssa aufwuchs densities on a unit area of bottom basis (Figures 5 and 6). However, this is probably attributable to the greater density of shrubs per square meter of bottom and not a greater density of crustaceans per unit area of Cephalanthus aufwuchs habitat.

When the benthic densities were added to the aufwuchs densities in the Nyssa zone, they were usually greater than the densities of the aufwuchs in the Cephalanthus zone, which had no benthic counterpart (Figures 7 and 8). However, the amphipod population reached a maximum mean density of $5244/m^2$ in the Nyssa zone in March and $8024/m^2$ in the Cephalanthus zone in May (Figure 7). These densities slowly declined to a mean density of $151/m^2$ in the Nyssa zone in October and $85/m^2$ in the Cephalanthus zone in January.

The isopod population reached a maximum mean density of $3140/m^2$

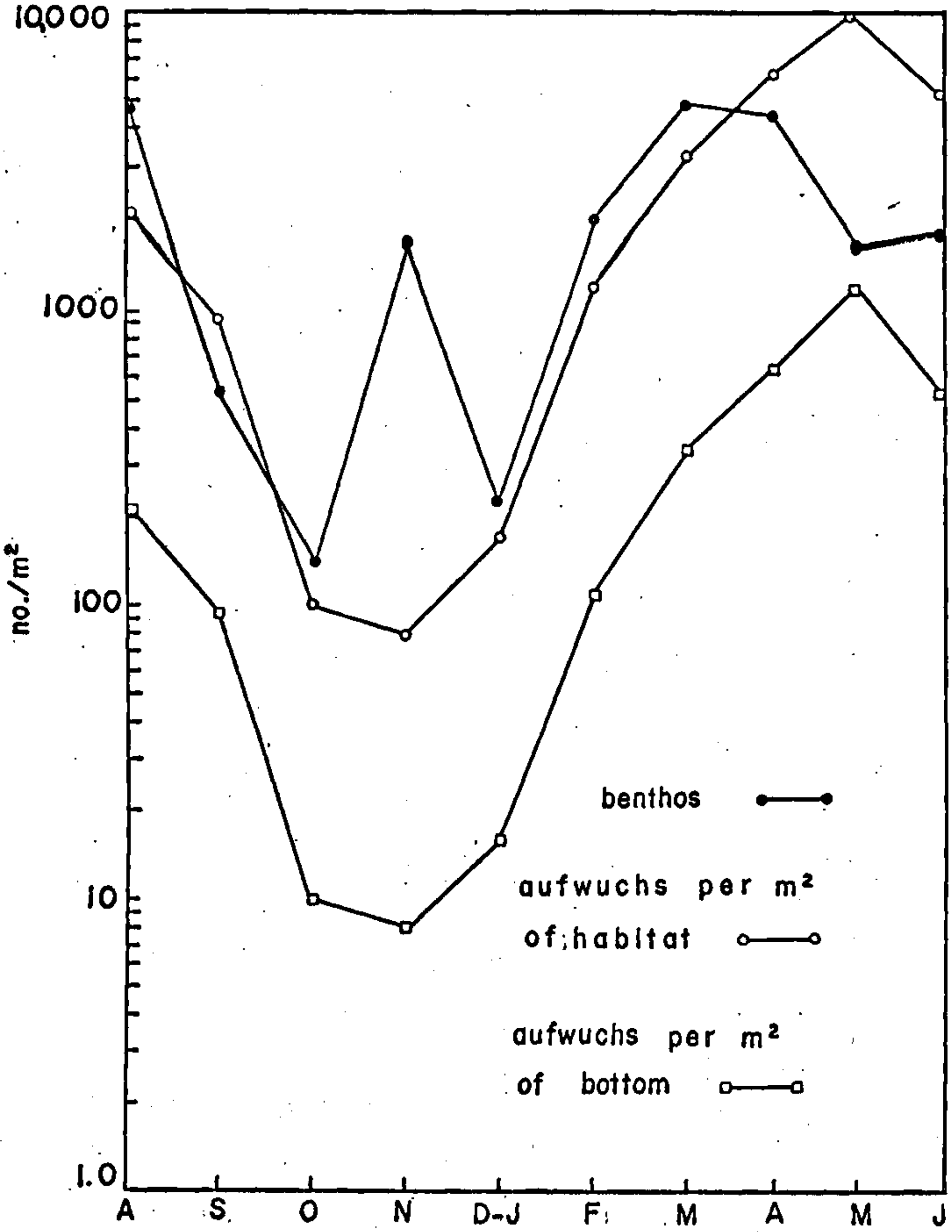

Figure 5. Comparison of Crangonyx gracilis Monthly Densities in the Benthos and Aufwuchs of the Nyssa biflora Zone.

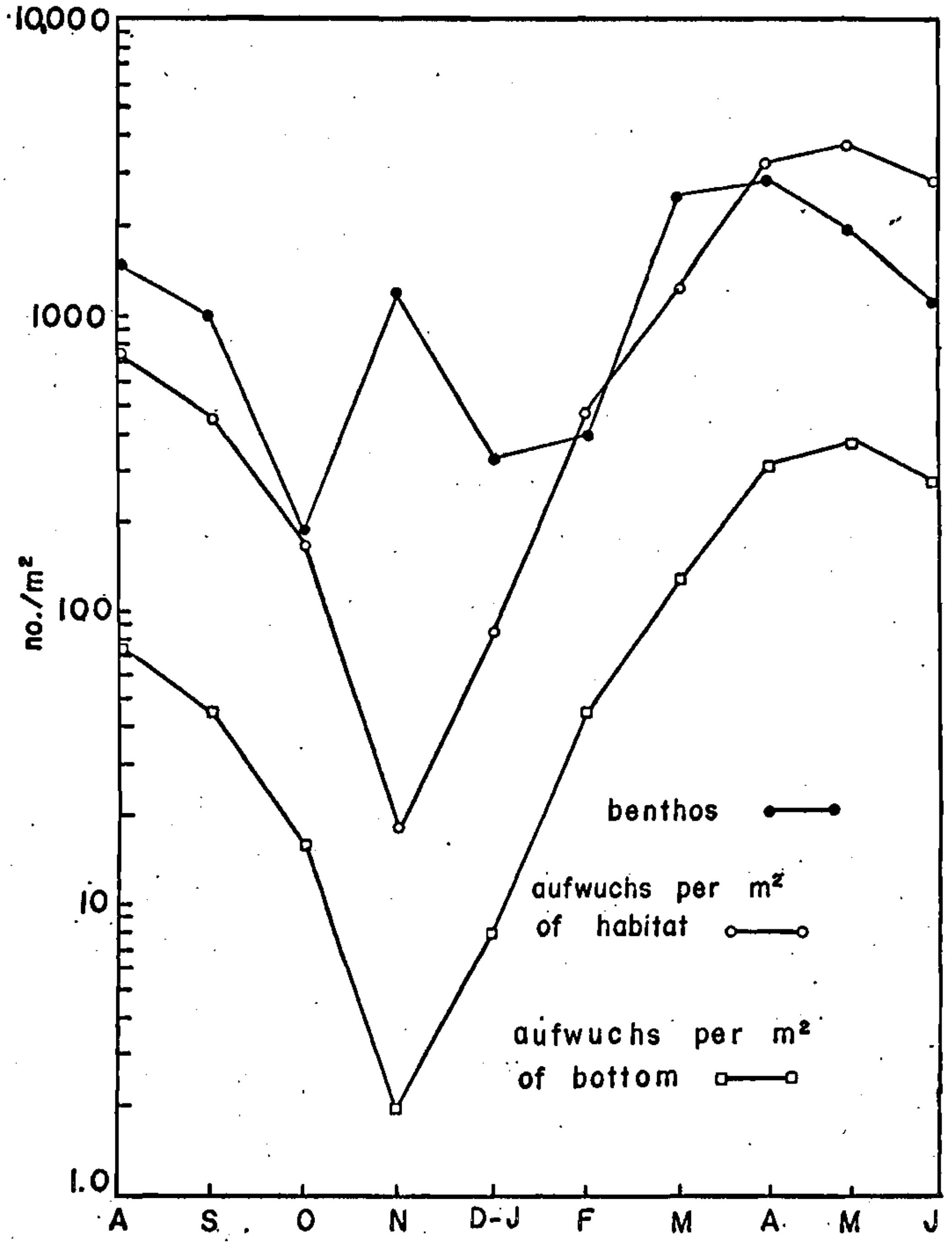

Figure 6. Comparison of Asellus obtusus Monthly Densities in the Benthos and Aufwuchs of the Nyssa biflora Zone.

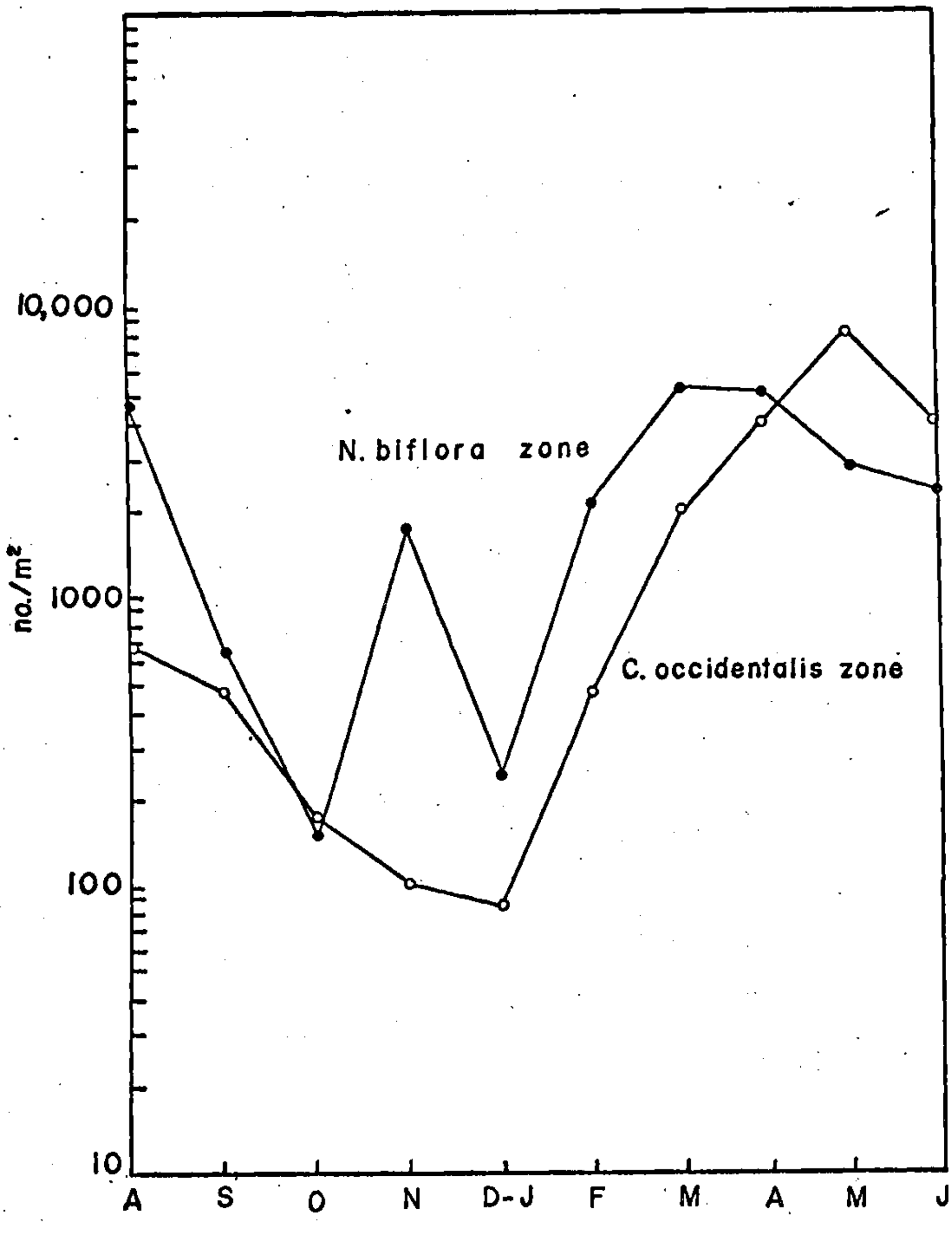

Figure 7. Comparison of Crangonyx gracilis Monthly Densities in the Nyssa biflora Zone (Benthos and Aufwuchs) and Cephalanthus occidentalis Zone (Aufwuchs Only) on a Per Square Meter of Bottom Basis.

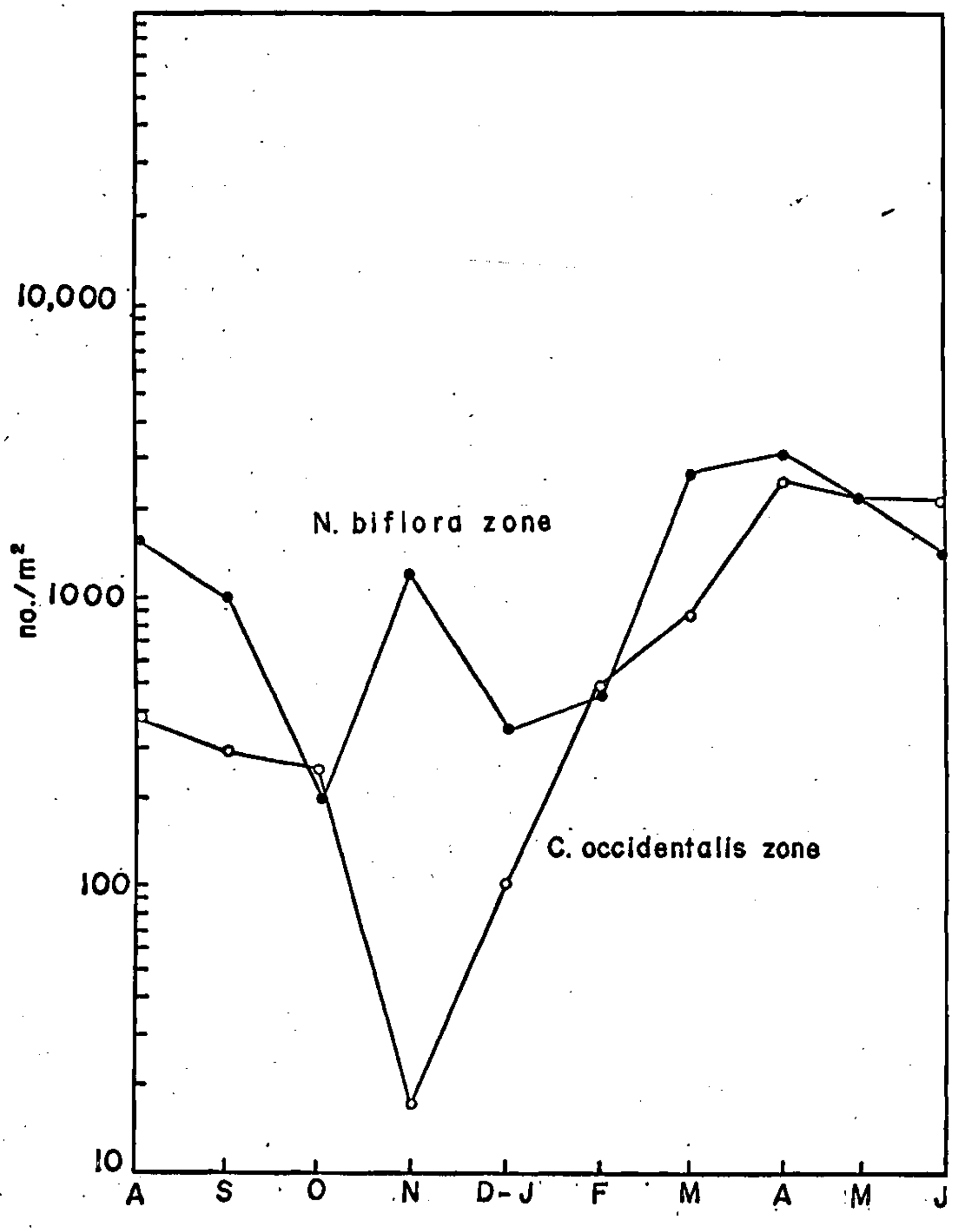

Figure 8. Comparison of Asellus obtusus Monthly Densities in the Nyssa biflora Zone (Benthos and Aufwuchs) and Cephalanthus occidentalis Zone (Aufwuchs Only) on a Per Square Meter of Bottom Basis.

in the Nyssa zone and $2533/m^2$ in the Cephalanthus zone in April (Figure 8). These densities then declined to a minimum mean density of $212/m^2$ in the Nyssa zone in October and $17/m^2$ in the Cephalanthus zone in November. In all samples crustacean densities showed a great deal of variation with the coefficients of variation ranging from 32% to 169%.

Biomass Determinations and Standing Crops

Regression analyses of the size-weight relations were made to obtain estimates of the mean weights of individuals for a given length. This information was used in the production and standing crop estimates. These relations were found to be double logarithmic. The logarithmic equation for weight (w), in milligrams, as a function of size (l), in millimeters of head length, for the amphipod is

$$\log w = .4882 + 3.9 \log l.$$

The equation for the isopod is

$$\log w = -.8564 + 2.8 \log l,$$

where w is in milligrams and l is in millimeters of abdominal width. These equations yield r^2 coefficients of .9793 and .9906 respectively.

Monthly standing crops were determined for each of the populations. These were computed using the monthly size frequency distributions and the mean individual weights for a given size class as determined by regression anslyses. The estimates for the amphipod (Figure 9) showed a monthly maximum standing crop of .72 g/m^2 in the *Nyssa* zone in March and .85 g/m^2 in the *Cephalanthus* zone in May. These correspond to the dates when maximum densities were attained in both zones respectively (Figure 7). Monthly minimum standing crops for *Crangonyx* occurred in October with a standing crop of .02 g/m^2 in the *Nyssa* zone and .02 g/m^2 in the *Cephalanthus* zone. The *Nyssa* minimum standing crop value corresponds to the date at which the lowest density was reached in this zone (Figure 7). In the *Cephalanthus* zone lowest densities were found in January, but with larger animals, there was greater biomass. Annual mean standing crops for the *Nyssa* zone and *Cephalanthus* zone were .40 g/m^2 and .23 g/m^2 respectively.

The isopod estimates (Figure 10) showed a monthly maximum standing crop of .72 g/m^2 in the *Nyssa* zone in November and .22 g/m^2 in the *Cephalanthus* zone in June. These do not correspond to dates when maximum densities were reached but this is due to differences in age structure and corresponding individual weights for the sampling dates. Monthly minimum standing crops were reached in October for the *Nyssa* zone with a value of .03 g/m^2 and in November for the *Cephalanthus* zone with a value of .006 g/m^2. These do correspond to the dates at which minimum densities were reached in both zones (Figure 8). Annual mean standing crops for the *Nyssa* zone and *Cephalanthus* zone were .24 g/m^2 and .09 g/m^2 respectively.

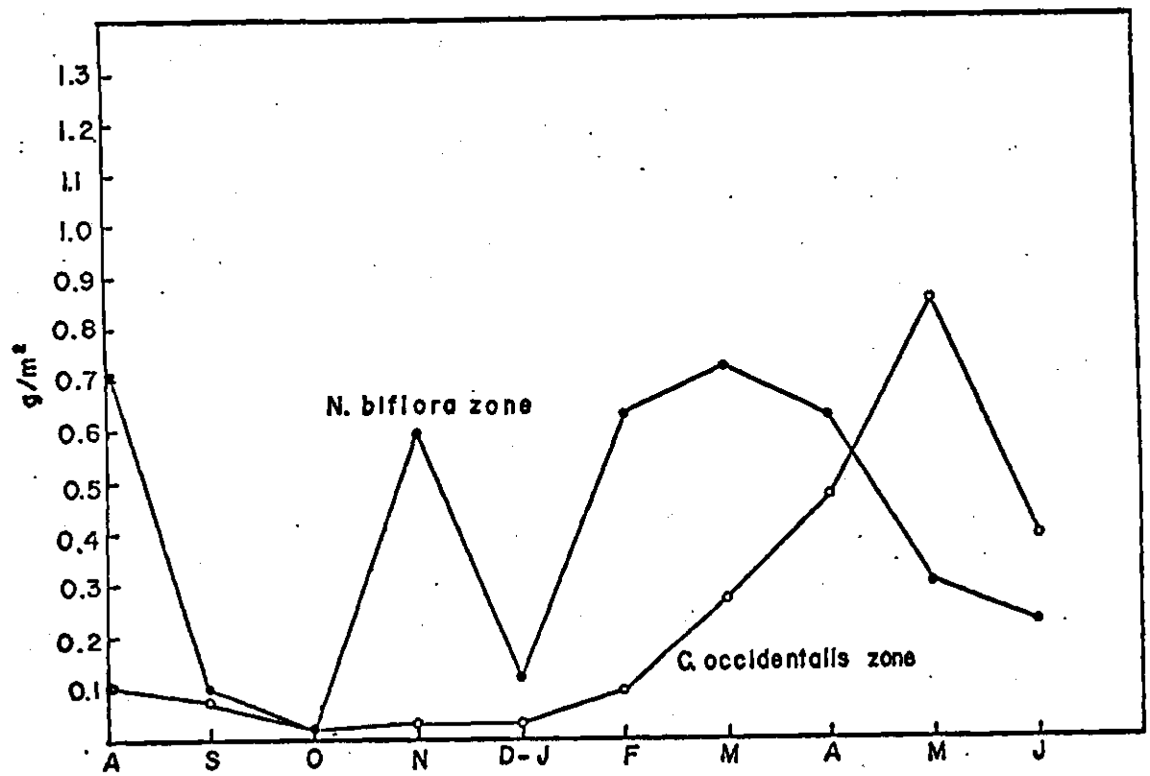

Figure 9. Comparison of Crangonyx gracilis Monthly Standing Crops in the Nyssa biflora Zone (Benthos and Aufwuchs) and Cephalanthus occidentalis Zone (Aufwuchs Only) as a Per Square Meter of Bottom Basis.

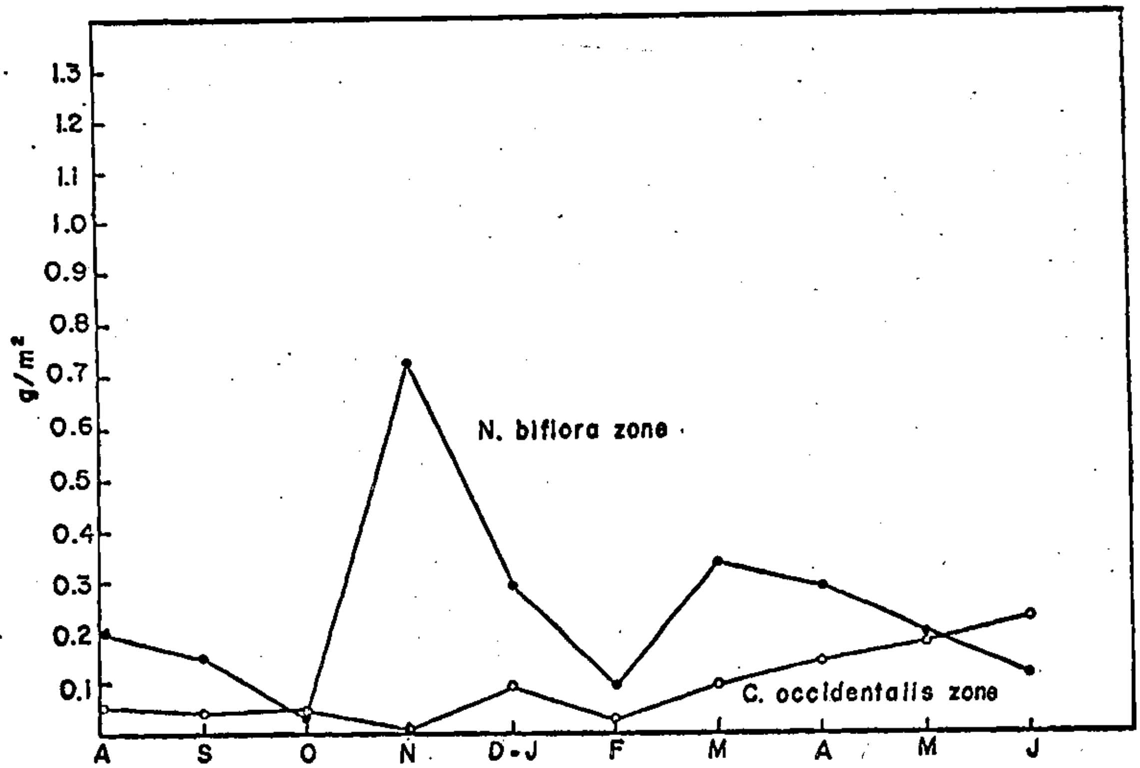

Figure 10. Comparison of Asellus Obtusus Monthly Standing Crops in the Nyssa biflora Zone (Benthos and Aufwuchs) and Cephalanthus occidentalis Zone (Aufwuchs Only) on a Per Square Meter of Bottom Basis.

Secondary Production of Crustaceans

Tables 1 and 2 illustrate the application of the Hynes and Coleman method to the amphipod data. The amphipod grows through a series of 10 size groups (based on head length). The numbers per square meter in each size group were estimated from field data collected over the year (column 2). The mean weight of each size group (column 3) was obtained from regression analysis of weight on size. The standing crop (column 4) for each size group was determined by multiplying numbers per square meter by the mean weight of an individual in that size group. The sum of the column is an estimate of the mean annual standing crop. Column 5 was calculated as the number loss per square meter between consecutive size groups. Column 6 is the weight at loss of an individual between adjacent size classes. This weight loss was calculated as the weight loss at the midlength point. For example, in Table 1 an individual that was lost between the first and second size class was assigned a weight at loss equal to the weight value midway between the weight of an individual in the first size class and one in the second size class (i.e., .044 mg is the midpoint between .025 mg and .064 mg). Column 5 multiplied by column 6 gives the weight loss for each size class in grams per square meter (column 7). The weight loss column must be multiplied by the number of size groups through which an individual grows (times loss factor), or 10 in this case, to yield production for each size group (column 8). The sum of this column is the annual production. Using the method

Table 1. <u>Crangonyx gracilis</u> Production in the <u>Nyssa biflora</u> Zone Using the Hynes and Coleman Method.

Size group (mm)	No./m^2	Mean wt. (mg)	Standing Crop (g/m^2)	No. less/m^2	Weight at less (mg)	Wt. less X 10 (g/m^2)	Production (g/m^2)
.26-34	738	.025	.0184				
				-100	.044	-.0044	-.0440
.34-.42	838	.064	.0536				
				473	.100	.0473	.4730
.42-.50	365	.137	.0500				
				31	.198	.0061	.0613
.50-.58	334	.259	.0865				
				228	.353	.0804	.8048
.58-.66	106	.448	.0474				
				56	.586	.0328	.3281
.66-.74	50	.724	.0362				
				23	.917	.0210	.2109
.74-.82	27	1.111	.0299				
				13	1.372	.0178	.1783
.82-.90	14	1.634	.0228				
				-2	1.977	-.0039	-.0395
.90-.98	16	2.320	.0371				
				10	2.758	.0275	.2758
.98-1.06	6	3.197	.0191				
				6	3.197	.0191	.1918

Standing crop = .40 g/m^2 Production = 2.44 g/m^2

Table 2. *Crangonyx gracilis* Production in the *Cephalanthus occidentalis* Zone Using the Hynes and Coleman Method.

Size group (mm)	No./m^2	Mean wt. (mg)	Standing crop (g/m^2)	No. less/m^2	Weight at less (mg)	Wt. less (g/m^2)	X 10 Production (g/m^2)
.26-.34	623	.025	.0155				
				-188	.044	-.0038	-.0387
.34-.42	811	.064	.0519				
				592	.100	.0592	.5920
.42-.50	219	.137	.0300				
				72	.198	.0142	.1425
.50-.58	147	.259	.0380				
				86	.353	.0303	.3035
.58-.66	61	.448	.0273				
				22	.586	.0128	.1289
.66-.74	39	.724	.0282				
				28	.917	.0256	.2567
.74-.82	11	1.111	.0122				
				6	1.372	.0082	.0823
.82-.90	5	1.634	.0081				
				-1	1.977	-.0019	-.0197
.90-.98	6	2.320	.0139				
				3	2.758	.0082	.0827
.98-1.06	3	3.197	.0099				
				3	3.197	.0095	.0959

Standing crop = .23 g/m^2 Production = 1.64 g/m^2

as outlined above, the amphipod had an estimated annual production of 2.44 g/m^2 from a mean annual standing crop of .40 g/m^2 (Table 1) in the _Nyssa_ zone. This yields a turnover ratio of 6.1. In the _Cephalanthus_ zone (Table 2) the estimated annual production was 1.64 g/m^2 from a mean annual standing crop of .23 g/m^2 yielding a turnover ratio of 7.1. The standing crop values obtained in this manner are the same as those mean annual values calculated from the mean monthly standing crops (Figure 9) which were .40 g/m^2 for the _Nyssa_ zone and .23 g/m^2 for the _Cephalanthus_ zone.

The production estimates for _Asellus_ (Tables 3 and 4) were carried out in the same manner as those for the amphipod. The only difference is that the isopod grows through a series of fifteen size groups (based on abdominal width) and this was used as the times loss factor in column 8 of Tables 3 and 4. The _Nyssa_ zone (Table 3) had an estimated annual isopod production of 1.43 g/m^2 and a mean annual standing crop of .24 g/m^2. These figures indicate a turnover ratio of 5.9 for this zone. Isopod production in the _Cephalanthus_ zone (Table 4) was estimated to be .65 g/m^2 from a mean annual standing crop of .08 g/m^2 yielding a turnover ratio of 8.1. These standing crop values also compare very well with the mean annual values obtained from the mean monthly standing crops (Figure 10) which were .24 g/m^2 for the _Nyssa_ zone and .09 g/m^2 for the _Cephalanthus_ zone.

The production values for _Asellus_ and _Crangonyx_ may be added

Table 3. Asellus obtusus Production in the Nyssa biflora Zone Using the Hynes and Coleman Method.

Size group (mm)	No./m^2	Mean wt. (mg)	Standing crop (g/m^2)	No. less/m^2	Weight at less (mg)	Wt. less X 15 (g/m^2)	Production (g/m^2)
.2-.4	247	.005	.0012	-57	.012	-.0006	-.0102
.4-.6	304	.020	.0068	88	.035	.0030	.0462
.6-.8	216	.051	.0110	64	.077	.0049	.0739
.8-1.0	152	.104	.0158	-10	.143	-.0014	-.0214
1.0-1.2	162	.182	.0294	93	.236	.0219	.3292
1.2-1.4	69	.290	.0200	2	.361	.0007	.0108
1.4-1.6	67	.433	.0290	35	.524	.0183	.2751
1.6-1.8	32	.615	.0196	6	.727	.0043	.0654
1.8-2.0	26	.840	.0218	4	.976	.0039	.0585
2.0-2.2	22	1.112	.0244	10	1.273	.0127	.1909
2.2-2.4	12	1.434	.0172	6	1.728	.0103	.1555
2.4-2.6	6	2.022	.0121	-2	2.134	-.0042	-.0640
2.6-2.8	8	2.247	.0179	4	2.496	.0099	.1497
2.8-3.0	4	2.745	.0109	2	2.881	.0057	.0864
3.0-3.2	2	3.018	.0060	2	3.018	.0060	.0905

Standing crop = .24 g/m^2

Production = 1.43 g/m^2

Table 4. Asellus obtusus Production in the Cephalanthus occidentalis Zone Using the Hynes and Coleman Method.

Size group (mm)	No./m^2	Mean wt. (mg)	Standing crop (g/m^2)	No. less/m^2	Weight at less (mg)	Wt. less (g/m^2)	X 15 Production (g/m^2)
.2-.4	167	.005	.0008	-56	.012	-.0006	-.0100
.4-.6	223	.020	.0044	36	.035	.0012	.0189
.6-.8	187	.051	.0095	93	.077	.0071	.1074
.8-1.0	94	.104	.0097	9	.143	.0012	.0192
1.0-1.2	85	.182	.0154	50	.236	.0118	.1770
1.2-1.4	35	.290	.0101	10	.361	.0036	.0541
1.4-1.6	25	.433	.0108	13	.524	.0068	.1021
1.6-1.8	12	.615	.0073	6	.727	.0043	.0654
1.8-2.0	6	.840	.0050	2	.976	.0019	.0292
2.0-2.2	4	1.112	.0044	3	1.273	.0038	.0572
2.2-2.4	1	1.434	.0014	0	1.728	0	0
2.4-2.6	1	2.022	.0020	1	2.134	.0021	.0320
2.6-2.8	0	2.247					
2.8-3.0	0	2.745					
3.0-3.2	0	3.018					

Standing crop = .08 g/m^2 Production = .65 g/m^2

together to give an estimate of the combined annual crustacean production in each zone. This gives a production estimate of 3.87 g/m^2 in the *Nyssa* zone and 2.29 g/m^2 in the *Cephalanthus* zone. Mean annual standing crop treated in same manner yields .64 g/m^2 in the *Nyssa* zone and .31 g/m^2 in the *Cephalanthus* zone. These figures indicate about a two fold difference in production and mean annual standing crops on a per unit area of bottom basis between the zones.

Total annual crustacean production of the zones may be estimated by multiplying the combined annual production per square meter by the area of the zones at average water level. Using these figures the total combined crustacean production is 11.668 kg for *Nyssa* zone and 1.213 kg for the *Cephalanthus* zone. Combined mean annual standing crop treated in the same manner yields 1.929 kg for the *Nyssa* zone and .164 kg for the *Cephalanthus* zone. This comparison indicates that on a total area basis the *Nyssa* zone is much more productive than the *Cephalanthus* zone.

CHAPTER IV

DISCUSSION

There have been a number of past studies dealing with the general aspects of the life histories of amphipods and isopods (Hynes 1955, Bousfield 1958, Ellis 1961, and Steel 1961). *Crangonyx gracilis* is an amphipod typically inhabiting small bodies of fresh water such as ponds, streams, and swamps (Pennak 1953, Holsinger 1972). There has been little work done on this species since Bousfield (1958) summarized most of the useful information and clarified its vague status. There still exists today some question regarding the taxonomy of this species (Holsinger, 1972) and it may be that it is actually composed of a complex of sub-species. For this reason the range of the species is not known except for scattered collections over the eastern United States. The isopod, *Asellus obtusus*, is an inhabitant of small bodies of fresh-water whose range is confined to a small area in the southeastern United States (Williams, 1972). Life history information is only available on related species (Ellis 1961, Steel 1961).

In the present study the most obvious of the general results concerning the crustacean populations are the differences between the two major vegetational zones in the ecosystem in terms of spatial distributions and productivity. Since differences in distribution cause related differences in productivity some of the possible factors causing variation in crustacean distributions will be discussed.

Spatial Distribution

Two factors appear to govern the distribution of crustaceans in Bob Black Pond. Oxygen concentrations were very low in deeper portions of the pond and crustacean densities were extremely low in these areas. Since oxygen concentrations in the aufwuchs and Nyssa benthic microhabitats were higher this would seem to partially explain the substantial densities found in these microhabitats.

Food availability may also play a role in determining spatial distributions. Mathias (1971) in studying energy flow and secondary production of amphipods in Marion Lake, British Columbia, pointed out that decreased densities in deeper portions of the lake may be due to a decrease in the amount of suitable energy substrates available to individuals. Amphipods and isopods are characterized as scavengers but they also feed on live material such as epibenthic algae (Pennak 1953, Ellis 1961). Hargrave (1970) has shown that the abundance of epibenthic algae decreases with depth in Marion Lake, B. C., and this may be a factor causing the decrease in amphipod densities with depth in this particular lake. Also, a study of crustaceans in a Kentucky stream (Minckley, 1963) indicated apparent symbiotic relations between an isopod and amphipod population. The isopods were found to frequently feed on the feces of the amphipods and, therefore, tended to frequently clump together. These same relations may be partially responsible for spatial distributions in Bob Black Pond.

Water Level Fluctuations

Most wetlands may be characterized by water level fluctuations (Helfgott, et al, 1973). These fluctuations may provide for a high productivity by furnishing an energy subsidy to the ecosystem (Odum, 1971). The lowering of the water level exposes organic material to the atmosphere allowing a rapid aerobic decomposition to take place in the moist environment (Wharton, 1970). Upon reflooding of the exposed material, nutrients are released into the water and provide substrates for growth, particularly aquatic plant growth.

Water level fluctuations are important in Bob Black Pond also. The water level fluctuations affect the habitat area in the *Nyssa* zone because not only does the benthic area change but many of the *Nyssa* are excluded from the aquatic phase of the system when the water recedes. The area of the *Cephalanthus* zone was not affected by these fluctuations except in a vertical manner. It was assumed that little or no migration took place between zones. This may not be entirely valid but because of the ecosystem structure it was thought to be reasonable.

The aquatic community is apparently adapted to general fluctuations in water level. One can see by the trends in monthly crustacean densities (Figures 7 and 8) in both the Nyssa and Cephalanthus zones that the densities more or less follow the regimen of the water level fluctuations. After the rise to maximum pool size in January, densities increase while water level is high, and then decline when the pool size begins decreasing in the summer. There is no aggregation of animals with declining pool size as one might have expected. However, November densities in the Nyssa zone seem to be higher. This increase in density did not occur either in the Cephalanthus zone or in the Nyssa aufwuchs densities (Figures 5 and 6). This leads to a suspicion of sampling error introduced in the estimation of this date's Nyssa benthic densities, especially since this apparent increase cannot be due to reproduction (Figures 3 and 4).

Although the data tend to indicate changes in area of available habitat would not affect production estimates made on a per unit area basis they would affect the estimation of the total production of the entire community. Total production estimates given earlier were based on the area of available habitat at average water level and these estimates will vary with water level fluctuations.

Biomass Determinations

Size-weight relations were well explained by regression analyses in view of the high r^2 values obtained for the least squares lines. The slope coefficient for the amphipod agrees closely with Mathias' (1971) coefficient of 3.89 for the amphipod Crangonyx richmondensis occidentalis. No comparable estimates for the isopod are available. As Winberg (1971) points out, the range of size over which these statistics were computed should be specified and the reader would do well to make note of this range by referring to the values of the size class intervals used in the production estimates.

Secondary Production of Crustaceans

Several methods are currently available for assessing secondary production of aquatic animals (Hynes and Coleman 1968, Hamilton 1969, Edmondson and Winberg 1971, Winberg 1971, and Waters and Crawford 1973). The methods are based on two general approaches: the direct approach in which measurements of actual population changes are made and the indirect approach based on the amount of food required to feed fish predators. Theoretically, the indirect methods should give underestimates since fish predation is only one of many sources of mortality. However, in practice, this approach has led to estimates of secondary production much higher than those obtained from the direct methods. Although many people using the direct methods believe indirect methods give overestimates, it very well may be that direct methods give underestimates (Benke, 1974).

There are four available methods in the direct approach category:

the instantaneous growth model, the graphical Allen curve method, the removal-summation method and the Hynes and Coleman (1968) method as modified by Hamilton (1969). A frequent problem with the first three methods lies in the necessity to be able to age an individual to determine growth rates or the identity of the cohort to which it belongs. Because of the difficulty of identifying specific cohorts in the present study, these methods could not be used and the Hynes and Coleman method for non-recognizable cohorts was used instead. Several errors in the original method were corrected by Hamilton (1969). Objections to this method have been made (Fager, 1969) but Waters and Crawford (1973) in their comparison of the above four methods concluded that the Hynes and Coleman method shows promise as a reliable and simple method, even though approximate.

In order to use the Hynes and Coleman method several assumptions must be met (Hamilton, 1969), two of which may be questioned in the present study. These are: (1) The species represented in the samples are univoltine, and (2) The species can potentially grow to the maximum size used in the size frequency distribution.

The validity of the latter assumption may be questioned by some because several investigators have found differences in the maximum size obtained by the different sexes in similar populations (Ellis 1961, Hynes 1955). In the present study no major size differences between sexes was detected through casual observation. Even if such differences did occur, this would introduce only a very minor error in the production estimates (Hamilton, 1969).

A more serious error could be introduced by not meeting the assumption regarding voltinism (Hamilton, 1969). In constructing size frequency distributions (Figures 3 and 4) one can get a picture of the reproductive cycle of the species involved. Both demonstrate an extensive reproductive period. Some of the late summer hatching is probably due to the breeding of spring individuals who have matured over the summer. Most work of this nature has been done in more northerly latitudes where the reproductive period is much shorter and the hatching peaks more distinct. Because of the indistinct peaks it was very difficult to ascertain how much of the above breeding activity was taking place. There is a strong possibility that considerable turnover is taking place during this period when age structure appears relatively stationary. It would seem that the inability to detect such turnover in a population is a major weakness of the Hynes and Coleman method as used in this study. If this is the case then error was introduced in the production estimates and the actual values are considerable understimates. However, the relative values of the habitat zones should be valid for the sake of comparison.

Andersson (1969) estimated the production of the isopod, Asellus aquaticus (L.), in two Swedish lakes using the removal-summation method. He estimated an annual production of 16.70 g/m^2 from a mean annual standing crop of 8.52 g/m^2 in one lake and a production of 31.69 g/m^2 from a mean annual standing crop of 15.59 g/m^2 in the other lake. These values yield annual turnover ratios of 1.96 and 2.03 respectively (two generations per year). Andersson's estimates were based on the wet weight of preserved animals and if one assumes that approximately 90% of the weight is body water then his estimates are comparable to those of the isopod in the present study.

Cooper (1965), using the growth rate method, estimated the production of the amphipod, Hyallela azteca, in a Michigan lake. His estimates indicated an annual production of 4.7 g/m^2 (dry weight) from a mean annual standing crop of .40 g/m^2. The turnover ratio was 11.6 (two generations per year). Mathias (1971) studied production of the amphipods, Hyallela azteca and Crangonyx richmondensis occidentalis, in a lake in British Columbia using the growth rate method. He found annual production in the shallow portions of the lake to be 1.8 g/m^2 (dry weight) from a mean standing crop of .39 g/m^2 for Hyallela azteca and a production of .34 g/m^2 (dry weight) from a mean annual standing crop of .19 g/m^2 for Crangonyx. These values yield annual turnover ratios of 4.6 and 1.8 respectively (one generation per year for both). The amphipod production in this study is comparable to these values but, with the exception of Cooper's estimates, the turnover ratios are higher. This was true of the turnover ratios for the isopods also. Waters (1969) states that most aquatic invertebrates have been found to have turnover ratios in the range of 2.5 to 5 with a mode of 3.5. However, Waters and Crawford (1973) in comparing production methods found that the Hynes and Coleman method gave a slightly higher annual turnover ratio than the other methods used.

The production values obtained do not seem particularly indicative of a high benthic productivity. A number of factors could cause underestimates to be made. Sampling error may have contributed to low estimates. An invalid assumption regarding the univoltine characteristics of the populations could cause a considerable underestimate. Also, certain areas of probable high production, such as Potamageton beds, were not included in the production estimates due to the difficulty of sampling these areas. On the other hand, perhaps the physico-chemical parameters and the advanced successional state of Bob Black are indicative of approaching dystrophy and consequently lowered productivity.

The majority of benthic invertebrate energy flow in Bob Black Pond takes place in the shallow Nyssa biflora zone in which aufwuchs and benthic microhabitats are in close proximity. The benthos of this zone contribute most of the energy flow. The remaining invertebrate energy flow takes place in the aufwuchs microhabitat of the deep Cephalanthus occidentalis zone. Aufwuchs production on a unit area of bottom basis is much less than benthic production. However, on a unit area of habitat basis the aufwuchs microhabitat may be more or less as productive as the benthic microhabitat if one can draw conclusions from the aufwuchs densities per unit of habitat area observed in the Nyssa zone (Figures 5 and 6). There have not been a great many hydrobiological studies dealing with the aufwuchs or periphytic portion of the aquatic community. In some systems it may not be important in relation to the other subsystems. However, in many wetlands this is an important component of the ecosystem. This paper serves to demonstrate that this component may play a substantial role in the total community metabolism.

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